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Diet influences the detoxification enzyme activity of *Bactrocera tau* (Walker) (Diptera: Tephritidae)

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Abstract: Detoxification enzymes in insects are generally demonstrated as the enzymatic defense against foreign compounds and play significant roles in maintaining their normal physiological functions. In this study, protein contents and carboxylesterase (CarE), acid phosphatase (ACP), alkaline phosphatase (ALP), cytochrome P450-dependent O-demethylase and glutathione S-transferase (GST) activities of *Bactrocera tau* Walker were determined by biochemical methods. The results showed that protein contents and these detoxification enzyme activities of the fruit fly varied significantly when fed on different diets including cucumber, pumpkin, towel gourd, white gourd and balsam pear. For protein contents, they were highest on balsam pear while lowest on cucumber and white gourd. For these detoxification enzymes, the CarE activity was highest on cucumber and pumpkin, cytochrome P450-dependent O-demethylase and GST activities were highest on balsam pear, but ACP and ALP activities were lowest on cucumber and pumpkin, respectively. In addition, these detoxification enzyme activities were also significantly different in the larval, pupal and adult stages. Adults had the highest CarE activity, and larvae had the highest ALP, cytochrome P450-dependent O-demethylase and GST activities, but the lowest ACP activity. Generally, these detoxification enzyme activities in the pupal stage were lower than those in the larval and adult stages except for ACP. Based on the above results, it was inferred that these detoxification enzyme activities were closely related to host plant species and developmental stages of this fruit fly.

Key words: *Bactrocera tau*; diet-insect interaction; detoxification enzyme activity

1 INTRODUCTION

Plants defend themselves from attacks by herbivorous insects in several ways. One important way is the chemical defence by toxic allelochemicals in plants such as organic cyanides, some terpenoids and alkaloids. These allelochemicals are commonly present in plants, and their composition and concentration differ greatly among different kinds of plants even their different growth stages (Visser, 1986). For herbivorous insects to survive on plants containing toxic allelochemicals, they must have the capacity to reduce the toxic effect to a nonfatal level. During the course of degrading or sequestrating toxic compounds especially some naturally occurring plant allelochemicals and organic pesticides, the detoxification enzymes, such as general esterases including carboxylesterase (CarE), acid phosphatase (ACP) and alkaline phosphatase (ALP), cytochrome P450 monooxygenases (P450s) and glutathione S-transferases (GSTs), play an important role (Gordon, 1961; Yang *et al*., 2001). Among them, esterases are those hydrolytic enzymes in which cleave esters made up of organic, mineral acid and alcohols or phenols (Michèle *et al*., 2000), P450s constitute a large superfamily of heme-thiolate proteins and play important roles in metabolism of a wide variety of endogenous and xenobiotic compounds (Siminszky *et al*., 1999; Doddapaneni *et al*., 2005), and GSTs are a group of enzymes involved in the detoxification process of herbicides and other substances in some plants (Reade and Cobb, 1999). Therefore, these detoxification enzyme activities in herbivorous insects are probably affected by plant allelochemicals, and affect the metabolism of pesticides because mechanisms that function in detoxification of plant allelochemicals in their diets may also be effective at detoxifying pesticides.

Bactrocera tau (Walker), which has broken out in Southeast Asia and the Pacific region, such as China, Japan, Thailand, Malaysia, Laos, Philippines, Cambodia, India, Bhutan, Indonesia and Sri Lanka,

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mainly infests cucumber, pumpkin, towel gourd, white gourd, balsam pear and other vegetables (Gupta *et al*., 1992; Allwood *et al*., 1999; Chinajariyawong *et al*., 2003). Since its outbreak in many regions, the pest has received considerable attention. The previous study on this fruit fly mainly concentrated on some ecological questions such as population fluctuations on cucumber, balsam pear, sponge gourd and bottle gourd (Gupta *et al*., 1992; Liu and Lin, 2001), population growths under different temperatures and photoperiod conditions (Zhou *et al*., 1994, 1995, 2005), and the effect of intraspecific competition on the population growth, development and survival (Zhou and Mei, 1999). These researches indicated that the growth, development and fecundity of this fruit fly were greatly influenced by kinds of diets and environmental factors. However, it was not clear whether the physiological response of the insect was also associated with specific diets and developmental stages of this fruit fly. Based on the reason stated above, we carried out the study, and the objective was to determine whether these detoxification enzyme activities of this fruit fly are related to kinds of diets, and whether there exist interactions between diets and developmental stages. This information in this study could be useful in the pest management on different host plants.

2 MATERIALS AND METHODS

2.1 Insect resources

Damaged gourds by *B*. *tau*, most of the genus *Cucumis* L., and some species of the genus *Luffa* L., *Benincasa* Savi., *Momordica* L., were collected from the field in June of 2005 in Beibei, Chongqing, China. Eggs and larvae in the damaged gourds were maintained in a rearing box under natural light conditions until the eclosion of adults. Voucher specimens were deposited at the insect collection of Southwest University, Chongqing, China.

2.2 Treatment of insects

A mixture of 100 female adults (15 day-old) from the above rearing box was transferred to a growth chamber containing five kinds of fresh gourds: cucumber, *Cucumis sativus* Linn; pumpkin, *Cucurbita moschala* Duch; towel gourd, *Luffa cylindrical* Roem; white gourd, *Benincasa hispida* (Thunb.) Coqn.; and balsam pear, *Momordica charantia* Linn. The gourds supplied for laying eggs were similar in weight (50 – 100 g per gourd). Two days later, these gourds with eggs were separated according to varieties and then maintained in different growth chambers at 28℃, RH 80% ± 5% and photoperiod of 14.00:10.00 hours (L:D), respectively. Larvae from the above gourds were reared on the respective gourd, and 5 – 8 cm depth soil layer was added to provide a pupation site for the mature larvae exiting these damaged gourds. During the course of rearing, 7 day-old larvae, 2 day-old pupae and 2 day-old adults used for the test were collected respectively and frozen at – 80℃ immediately.

2.3 Enzyme preparation

For CarE preparation, fruit flies selected arbitrarily from the progeny of 100 individuals were homogenized in 0.04 mol/L, pH 7.0 ice-cold sodium phosphate buffer according to the ratio of the fruit fly to sodium phosphate buffer 1∶10 (g/mL). The crude homogenate was centrifuged at 10 000 g for 15 min at 4℃. The supernatant fluid was diluted 1∶10 with the above buffer before being used.

For ACP preparation, fruit flies were homogenized in 0.2 mol/L, pH 4.6 acetic acid buffer in terms of the ratio of the fruit fly to acetic acid buffer 1∶10 (g/mL). The crude homogenate was centrifuged at 10 000 g for 10 min at 4℃. The supernatant fluid was diluted 10 times, and then used in the assays. For ALP, barbital sodium-hydrochloric acid (0.04 mol/L, pH 8.9) was used as the homogenization buffer and other procedures were similar to that used for ACP.

For P450s preparation, fruit flies were homogenized in ice-cold sodium phosphate buffer (0.2 mol/L, pH 7.8) according to the ratio above-mentioned. The homogenate was filtered through two layers of cheesecloth and then centrifuged at 300 g for 5 min at 4℃. The supernatant was centrifuged for 8 min at 2 000 g and quickly kept at 4℃ before being used (Kim *et al*., 1996). For GST, Tris-HCl (0.05 mol/L, pH 7.5) was used as the homogenization buffer, and other procedures were similar to that used to CarE.

2.4 Protein estimation

The total protein content in supernatants was determined by the method of Bradford (1976) using a Tecan Sunrise Microplate Reader (Tecan, Austria). The incubation mixture consisted of 0.8 mL of phosphate buffer (0.2 mol/L, pH 6.8), 5.0 mL of Coomassie blue solution G-250 (0.0025%) and 0.2 mL of enzyme solution. A total of 0.3 mL of the incubation mixture was transferred to the well of a 96-well microtiter plate, and then the absorbance was read at 595 nm, 25℃ against a blank lacking protein and compared to a bovine serum albumin (BSA) standard curve. The experiment was replicated 3 times using different supernatant each time.

2.5 Assay of enzyme activity

The CarE activity was assayed with p-naphthyl acetate (PNPA) as substrate according to the method described by van Asperen (1962). The incubation mixture contained 0.3 mL of supernatants, 5.0 mL of substrate (0.3 mmol/L), and 0.7 mL of sodium phosphate buffer (0.04 mol/L, pH 7.0). The reaction mixture was incubated for 30 min at 37℃ and terminated by the addition of 1.0 mL of freshly prepared Fast Blue B salt-sodium dodecyl sulphate solution. A total of 0.3 mL of the reaction mixture was transferred to the well and the absorbance was read 30 min later at 600 nm with the microplate reader. Three replications were done to determine the activity of this enzyme using different supernatant each time. Quantification of enzymatic product was based on a standard curve prepared with p-naphthol. One unit of CarE activity is defined as the amount of p-naphthol produced per mg protein in 30 min (Zhang *et al*., 2004).

The ACP and ALP activities were determined with 4-nitrophenyl phosphate disodium salt as substrate using the method introduced by Bessy *et al*. (1946). A total of 0.3 mL of enzyme solution was added to 1.7 mL of reaction solution containing 0.5 mL of substrate (0.0075 mmol/L). NaOH was added to stop the reaction after the mixture had been incubated for 30 min at 37℃. 0.3 mL of the above mixture was included in the well and variations in optical density were recorded at 400 nm by the microplate reader. Three replications were done to measure the activity of this enzyme. Quantification of enzymatic product was based on a standard curve prepared with p-nitrophenol. One unit of ACP or ALP activity is the amount of p-nitrophenol produced per mg protein in 30 min (Zhang *et al*., 2004).

The cytochrome P450-dependent O-demethylase activity was measured using p-nitroanisole as substrate by the method of Han *et al*. (2003). The incubation mixture contained 1 mL of enzyme solution, 0.5 mL of NADPH at a concentration of 1 mmol/L in sodium phosphate buffer solution, 0.1 mL of p-nitroanisole at a concentration of 0.1 mmol/L in the same buffer solution and 2.5 mL of the buffer solution. The mixture was shaken during incubation at 30℃ for 30 min, then the reaction was stopped by the addition of 1 mmol/L, 1.0 mL of HCl. 5 mL of chloroform was added with shaking to the mixture and 3 mL of the chloroform layer contained 4-nitrophenol isolated from chloroform extract was pipetted into a new tube. Subsequently, 0.5 mol/L, 3 mL of NaOH was added to the chloroform extract solution, and then 0.3 mL of the aqueous phase was transferred to the well of a 96-well microtiter plate. The variations in optical density were recorded immediately at 405 nm by the microplate reader. Three replications were done and the cytochrome P450-dependent O-demethylase activity quantified by a standard curve prepared with p-nitrophenol and the protein content in supernatants.

The GST activity was determined by the method described by Rauch and Nauen (2004) with 2, 4-dinitro chlorobenzene (CDNB) as substrate. The substrate is commonly used to measure the GST activity because GSTs mediate a reaction between CDNB and glutathione. Each well of microtiter plates was added to 0.1 mL of supernatant fluid, 0.1 mL of glutathione at a concentration of 12 mmol/L in distilled water and 0.1 mL of 1.2 mmol/L substrate. The variation of absorbance was monitored immediately at 340 nm every 30 s for 5 min to avoid the non-enzymatic reaction of CDNB and glutathione. The experiment was replicated 3 times using different supernatant each time, and the GST activity was calculated based on the following equations:

Units of enzymatic activity $(\mathrm{nmol} \cdot \mathrm{min}^{-1}) = (\Delta OD_{340} \cdot \nu)/(\varepsilon \cdot L)$

Where ΔOD_{340} is the variation value of absorbance per minute (ΔOD_{340}/min); ν equals the volume of reaction mixture; ε is the extinction coefficient of product [0.0096 L/(μmol·cm)]; and L (1 cm) is the length of optical path. The GST specific activity equals the specific value between the unit of enzymatic activity and the protein content of the supernatant fluid (Yang *et al*., 2001).

2.6 Data analysis

Activity levels of detoxification enzymes among different stages of the fruit fly reared on different host plants were analyzed by two-way analysis of variance (ANOVA) followed by Fisher's LSD test using the SPSS program. Factors for the two-way analyses were kinds of diets and developmental stages of the fruit fly.

3 RESULTS

3.1 Protein estimation

Protein contents of larvae, pupae and adults fed with diets cucumber, pumpkin, towel gourd, white gourd and balsam pear were presented in Table 1. Two-way ANOVA showed that the protein content of this fruit fly differed significantly among the five kinds of diets ($F = 40.04$; $df = 4, 30$; $P < 0.0001$) and the three developmental stages of the fruit fly ($F = 683.45$; $df = 2, 30$; $P < 0.0001$). The interaction between diets and developmental stages was also significantly different ($F = 41.0478$; $df = 8, 30$; $P < 0.0001$). The protein content was highest on balsam pear, and lowest on cucumber and white gourd. In addition, the protein content was highest at the larval stage, then the adult stage. The value of protein contents of this fruit fly provided the feasibility of calculating the activity of these enzymes.

Table 1 Protein contents in *Bactrocera tau* fed on different diets

Diets	Protein contents in *B. tau* (mg/g)		
	Larvae	Pupae	Adults
Cucumber	51.1534 ± 0.3835 b	33.7643 ± 0.4951 d	33.3628 ± 0.8284 c
Pumpkin	57.5221 ± 0.6642 a	35.4720 ± 0.3672 bc	38.5398 ± 0.8503 b
Towel gourd	47.1681 ± 0.7670 c	34.5133 ± 0.4951 cd	42.3746 ± 0.7906 a
White gourd	45.6342 ± 0.5423 c	36.0472 ± 0.2214 b	39.3068 ± 0.6549 b
Balsam pear	51.7699 ± 0.7670 b	44.4838 ± 0.4951 a	39.7198 ± 0.9587 b

Data (mean ± *SE*) in the same column followed by a common letter do not differ significantly ($P > 0.05$) according to Fisher 's LSD test.

3.2 Detoxification enzyme activity

There were significant differences on the CarE activity of this fruit fly among the five kinds of diets ($F = 303.04$; $df = 4, 30$; $P < 0.0001$) and three stages of the fruit fly ($F = 1117.81$; $df = 2, 30$; $P < 0.0001$). The CarE activity in this fruit fly reared on cucumber and pumpkin was higher than those on the other three diets, and the activity at the adult stage was highest among the three stages. In addition, the interaction between diets and stages was also significantly different ($F = 56.22$; $df = 8, 30$; $P < 0.0001$) (Fig. 1).

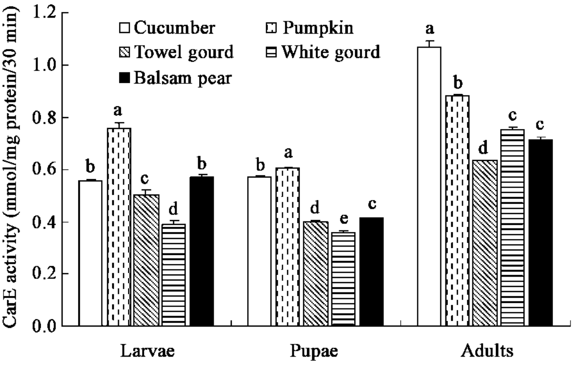

Fig. 1 CarE activities (mean ± *SE*) in *Bactrocera tau* fed on different diets

Bars with the same letter are not significantly different (Fisher 's LSD, $P > 0.05$). The same for the following figures.

The ACP activity varied significantly in different diets ($F = 41.1054$; $df = 4, 30$; $P < 0.0001$) and three stages ($F = 1690.4763$; $df = 2, 30$; $P < 0.0001$) based on the two-way ANOVA. The interaction between diets and stages was also significantly different ($F = 112.47$; $df = 8, 30$; $P < 0.0001$). The ACP activity was lowest significantly on cucumber among the above diets. In addition, the activity at the larval stage was significantly lower than those of pupae and adults (Fig. 2).

The ALP activity was significantly different in these diets ($F = 34.69$; $df = 4, 30$; $P < 0.0001$), as well as three stages of this fruit fly ($F = 491.00$; $df = 2, 30$; $P < 0.0001$). In addition, the interaction between diets and stages was also significantly different ($F = 47.61$; $df = 8, 30$; $P < 0.0001$). The ALP activity was lowest on pumpkin and highest on towel gourd and balsam pear among these diets, but the activity was highest at the larval stage in these diets (Fig. 3).

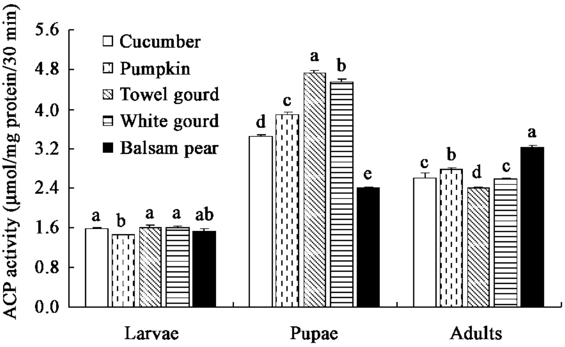

Fig. 2 ACP activities (mean ± *SE*) in *Bactrocera tau* fed on different diets

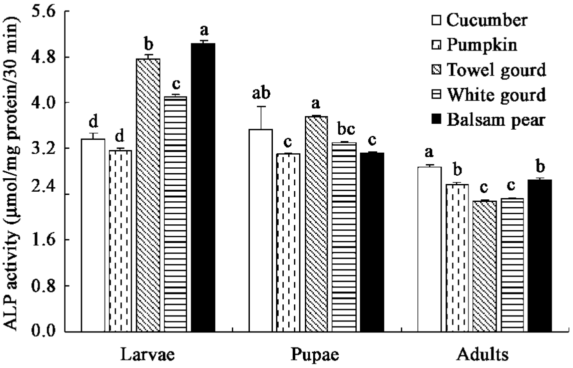

Fig. 3 ALP activities (mean ± *SE*) in *Bactrocera tau* fed on different diets

The two-way ANOVA showed that the cytochrome P450-dependent O-demethylase activity varied significantly among the above-mentioned diets ($F = 85.76$; $df = 4, 30$; $P < 0.0001$), the three stages of the fruit fly ($F = 1705.24$; $df = 4, 30$; $P < 0.0001$) as well as the interaction between diets and stages ($F = 4.75$; $df = 4, 30$; $P = 0.0004$). The cytochrome P450-dependent O-demethylase activity was highest when the fruit fly was reared on balsam pear, then on pumpkin and white gourd, and lowest on cucumber and towel gourd. The activity at the larval stage was markedly higher than those at pupal and adult stages (Fig. 4).

The GST activity of larvae, pupae and adults on

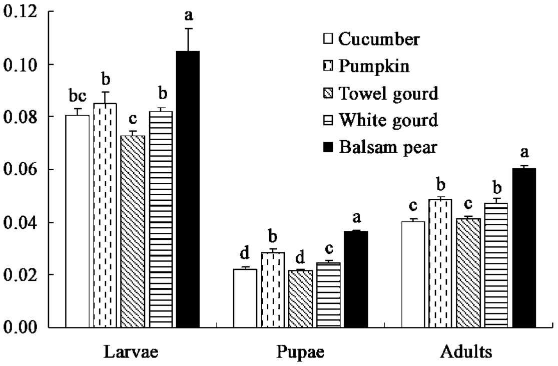

Fig. 4 Cytochrome P450-dependent O-demethylase activities (mean ± *SE*) in *Bactrocera tau* fed on different diets

each diet is presented in figure 5. The two-way ANOVA showed that the GST activity was significantly different in different diets ($F = 13.11$; $df = 4, 30$; $P < 0.0001$), as well as three stages ($F = 318.57$; $df = 2, 30$; $P < 0.0001$). In addition, the interaction between diets and stages was also significantly different ($F = 5.51$; $df = 8, 30$; $P = 0.0003$). The GST activity was higher on cucumber and balsam pear at each stage of the fruit fly, but the activity was highest at larval stage in the five kinds of diets (Fig. 5).

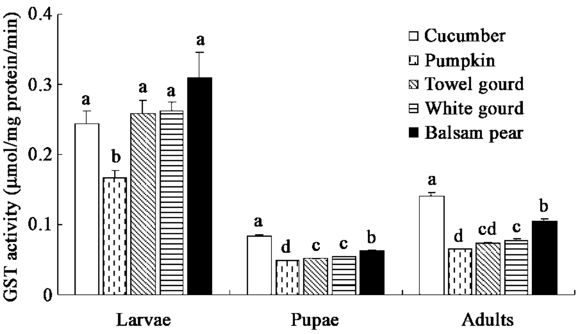

Fig. 5 GST activities (mean ± *SE*) in *Batrocera tau* fed on different diets

4 DISCUSSION

B. *tau* is a highly polyphagous insect and experiences a wide array of different compounds including some toxic allelochemicals in its use of more than 70 plant species (Christenson and Foote, 1960). It implies that this insect has the capacity to degrade those toxic allelochemicals in their diets. During the course of degrading toxic substances, the activities of some enzymes especially detoxification enzymes might be activated by some specific compounds in their diets. The present study confirmed that the CarE activity was highest when this fruit fly was reared on cucumber and pumpkin, but cytochrome P450-dependent O-demethylase and GST activities were highest on balsam pear among the five kinds of diets, *i.e.*, cucumber, pumpkin, towel gourd, white gourd and balsam pear. The possible mechanisms of these detoxification enzyme activities in relation to host plants were that the composition and concentration of detrimental chemicals for this fruit fly were different in different host plants, so correspondingly these enzyme activities changed as they fed on different host plants. Therefore, it is very necessary to determine the composition and concentration of allelochemicals in different host plants to understand the relation between detoxification enzyme activities and specific allelochemicals. To my regret, the composition and concentration of allelochemicals in those host fruits did not be assayed in this paper.

Insects can metabolize and thereby degrade toxic or detrimental chemicals for surviving in a chemically unfriendly environment. While all insects probably possess the capacity to detoxify detrimental chemicals, the amount can be expected to vary among insect species, with developmental stage of insects, and with the nature of insect's recent environment (Sívori *et al*., 1997). Our studies found that the detoxification enzyme activity of *B*. *tau* was positively correlated with its developmental stage except for the effect of kinds of diets. The results showed that adults had the highest CarE activity, and larvae had the highest cytochrome P450-dependent O-demethylase, GST and ALP activities, but the lowest ACP activity. However, changes of these detoxification enzyme activities were not clearly linked among its developmental stages, reinforcing the complex relationship between the insect and the chemistry of its host.

P450s are heme-thiolate proteins that catalyze the oxygenation of a broad spectrum of organic compounds (Brown *et al*., 2003). Among them, the cytochrome P450-dependent O-demethylase is one of the important oxidative reactions (Zhou *et al*., 2003). In this paper, the cytochrome P450-dependent O-demethylase activity using p-nitroanisole as substrate was determined when *B*. *tau* was reared on different diets. However, substrates of P450s are extremely diverse, and the P450 activities are different under the function of different substrates. At the same time, the P450 activities in herbivorous insects are also affected by the nutritional status of its host plants, the composition and concentration of allelochemicals in host plants, developmental stages of insects and other environmental conditions. Hence, the further experiments should be performed to accurately elucidate the change of the P450 activities at different conditions.

The detoxification enzyme activity has been known to be an important factor with respect to insecticide resistance in several insects (Yu, 1984). Many plant toxins or allelochemicals can induce or inhibit the activity of detoxification enzymes（Hung *et al*.，1990；Lee，1991）. Furthermore，the diversity and variability in composition and concentration of plant allelochemicals（e.g.，plant variety，growth condition，plant part and season）may impose a corresponding phenotypic and genotypic diversity and flexibility on detoxifying capabilities of insects（Brattsten，1988）. Brattsten *et al*.（1977）reported that some naturally occurring substances in host plants increased the activity of P450s，thereby reducing the susceptibility of larvae of southern armyworm，*Spodoptera eridania*（Cramer），to insecticides. In addition，plant secondary chemicals have been shown to have an effect on toxicity of azinphosmethyl（Berry *et al*.，1980；Yu，1986）. The study about the effect of diets on the detoxification enzyme activity of *B*. *tau* has revealed that the activities of CarE，ACP，ALP，cytochrome P450-dependent O-demethylase and GST were closely related to its host fruits and the developmental stage of this fruit fly. Thus，the information on host plants associated with the detoxification enzyme activity in this fruit fly could prove valuable in increasing the effectiveness of the pest control with insecticides.

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食料对南亚果实蝇解毒酶活力的影响

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摘要：昆虫解毒酶是一类异质酶系，对分解大量的内源或外源有毒物质、维持正常生理代谢起着重要作用。本文采用生物化学的方法测定了 5 种寄主果实对南亚果实蝇 *Bactrocera tau* Walker 3 个虫态体内总蛋白含量和 5 种解毒酶的活力。双因子方差分析显示，南亚果实蝇种群取食黄瓜 *Cucumis sativus* L.、南瓜 *Cucurbita moschala* L.、丝瓜 *Luffa cylindrical* L.、冬瓜 *Benincasa hispida*（Thunb.）Coqn. 和苦瓜 *Momordica charantia* L. 后，体内蛋白含量和解毒酶活性均存在显著差异。以丝瓜为食料时，南亚果实蝇体内蛋白含量较高；而以黄瓜和冬瓜为食料时蛋白含量则相对较低。在以上 5 种寄主果实间，南亚果实蝇的羧酸酯酶（CarE）活性在黄瓜和南瓜上较高，细胞色素 P450 O-脱甲基和谷胱甘肽 S-转移酶（GST）活性在苦瓜上较高，酸性磷酸酯酶（ACP）和碱性磷酸酯酶（ALP）活性却分别在黄瓜和南瓜上较低。在幼虫、蛹和成虫 3 个虫态间，解毒酶活性亦存在显著差异，成虫具有较高的 CarE 活性；幼虫具有较高的细胞色素 P450 O-脱甲基，GST 和 ALP 活性，但具有较低的 ACP 活性；除 ACP 外，蛹期解毒酶活性均较低。据以上结果可以推测，南亚果实蝇解毒酶活力受寄主果实种类以及该种群本身发育阶段的影响。

关键词：南亚果实蝇；食料-昆虫的相互作用；解毒酶活性

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